Habitat Preferences of Port Jackson Sharks, *Heterodontus portusjacksoni*, in the Coastal Waters of Eastern Australia.

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The habitat preferences of juvenile and adult *Heterodontus portusjacksoni* and ovipositing females were determined from three locations on the central and southern coast of New South Wales. Adults use shallow coastal rocky reefs in July-November for mating and oviposition, whilst juveniles occupy a seagrass nursery in a large coastal embayment. The sand/reef interface on the lee side of reefs was preferred by both sexes, probably as a refuge against strong water movements. Adult females also preferred rocky gutters when available, possibly as a male avoidance strategy. Preferred oviposition sites were narrow, shallow crevices (single capsules) or deep, narrow crevices (multiple capsules) which afforded protection against mechanical dislocation and/or predation. Juveniles exhibited a strong preference for the seagrass bed edge within a shallow nursery area. The visual complexity of this habitat combined with the juvenile's disruptive colouration may provide a refuge from predation, whilst proximity to the seagrass may provide ease of access for foraging. At a large scale, juveniles preferred areas of moderate slope within the nursery that provided protection from strong water movement. This study highlights the need for quantitative studies addressing habitat preferences and a consideration of use-specific factors to fully understand the selection of habitat by elasmobranchs.

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KEYWORDS: elasmobranchs, habitat use, habitat preferences, nursery area, oviposition.

INTRODUCTION

'Habitat' is the location or environment in which an organism lives and is determined by a complex interaction of physical and biotic factors (Sims 2003). Consequently, the range of habitats utilised by elasmobranchs and the factors contributing to their selection are many and diverse (Last and Stevens 1994; Goldman and Anderson 1999; Matern et al. 2000; Peach 2002). For example, Heithaus et al. (2002) found that prey availability was important to tiger sharks, *Galeocerdo cuvier*, while bat rays, *Myliobatis californica*, made daily movements between areas of different water temperature to thermoregulate and influence their metabolic rates (Matern et al. 2000). Consequently an understanding of habitat requirements is important for management and conservation. However, a complete understanding of the importance of habitat to a species requires the separation of habitat use from habitat preference (Carraro and Gladstone 2006). Use relates to the habitats in which individuals occur, whilst habitat preference is the level of utilisation of the habitat as a function of its relative availability.

Few detailed, quantitative studies of elasmobranch habitat utilization and preferences have been made and most have only involved overlaying movement data over gross habitat characteristics (Simpfendorfer and Heupel 2004). Despite this there is a clearly recognized need for a detailed understanding of habitat requirements for effective conservation and management, such as the selection and design of marine protected areas and assessments of the potential impacts of habitat degradation.

Many sharks show ontogenetic differences in habitat utilisation (Sündstrom et al. 2001). In most cases adult and juvenile populations are separated spatially, with juveniles and neonates occupying distinct nursery areas associated with decreased predation risks (Heupel and Hueter 2002) and possibly abundant food (Castro 1993). Juvenile and neonate blacktip sharks, *Carcharhinus limbatus*, in Terra Ceia Bay, Florida inhabited a core portion of their nursery area to avoid predation but made regular

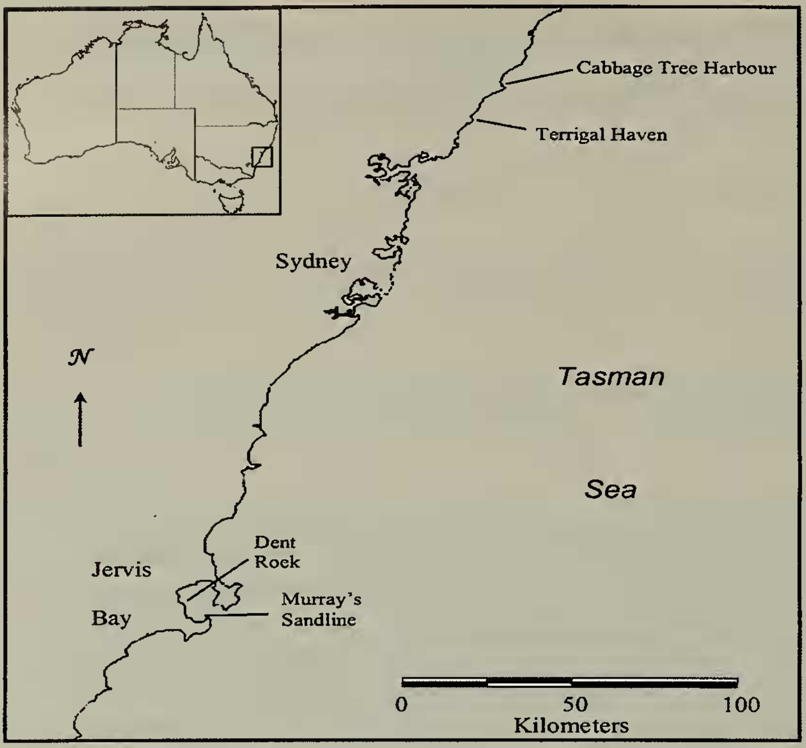

Figure 1: Map of the central and south coast of NSW, Australia showing the location of the study sites. Inset map shows the section of the east Australian coast depicted in the main figure.

excursions outside that area which were believed to be feeding forays (Heupel et al. 2004).

Adult *Heterodontus portusjacksoni* are demersal sharks that use a range of habitats throughout their life cycle (Powter 2006). Adult males and females migrate annually in the austral winter-spring (July-November) from deep offshore waters to shallow coastal rocky reefs for mating, oviposition and feeding. McLaughlin and O'Gower (1971) and O'Gower (1995) described the physical characteristics of resting sites as highly variable, however their studies were not quantitative and diel variations were not investigated. Additionally, habitat was considered in terms of use alone and did not relate habitat utilisation to availability. Similarly *H. portusjacksoni* oviposition areas were only described qualitatively (McLaughlin 1969). Viable capsules were securely wedged between rocks or in rock crevices on shallow rocky reefs in sheltered bays in depths from 1 to 20 m and occasionally on sheltered areas of some inshore reefs (McLaughlin 1969; Rodda 2000). However, no quantitative understanding exists of habitat preferences affecting the selection of oviposition areas by *H. portusjacksoni* or, in fact, for any oviparous elasmobranch. Finally, it remains unclear whether juvenile *H. portusjacksoni* utilise distinct nursery areas and, if so, what the specific features of these may be.

The first goal of this study was to determine the macro- and microhabitat features affecting habitat utilisation by *H. portusjacksoni* at adult reproductive grounds, the juvenile nursery area and oviposition sites and to elucidate any temporal, spatial or sex-based patterns. The second goal was to determine the habitat preferences of adult and juvenile *H. portusjacksoni* on the basis of utilised resting positions.

MATERIALS AND METHODS

Study sites

Observations on adults occurred at Cabbage Tree Harbour, Terrigal Haven and Dent Rock on the central and south-eastern coast of New South Wales (NSW), Australia (Fig. 1). Oviposition sites were studied at the latter two locations. The juvenile nursery area was located at Murray's Sandline, Jervis Bay, NSW (Fig. 1).

The three adult sites consisted of rocky reefs adjoining barren sand flats, with the junction between the two termed the interface. All sites were divided into macrohabitat zones on the basis of topography, substrate type and biotic characteristics.

Cabbage Tree Harbour (33°16' S, 151°34' E) is a shallow embayment, with water temperatures ranging from 15° C (mean ± S.E.; 16.6° C ± 0.37; n=7) in July to 18° C (16.6° C ± 0.40; n=5) in November during this study. The surveyed site extended for 270 m and was divided into three macrohabitat zones (west to east): (1) the wall zone (3.5–5.4 m deep) was characterised by a vertical rock wall with urchin-dominated barren boulders (Edgar 2001) and kelp (*Ecklonia radiata* and *Phyllospora comosa*) habitats at the far eastern end; (2) the boulder zone (5.4–6.0 m) was a gently sloping boulder field which is largely urchin barrens habitat with some *E. radiata* at the western edge; (3) the gutter zone (6.0–8.3 m) had a vertical rock wall above a steeply sloping boulder field with five narrow rock gutters ranging from 5–15 m long in 6–6.5 m depth at the eastern end.

Terrigal Haven is a shallow rocky reef in a small coastal embayment, with water temperatures ranging from 15° C (mean ± S.E.; 16.7° C ± 0.14; n=25) in July to 20° C (18.5° C ± 0.22; n=19) in November during this study. The surveyed reef extended for 280 m and was divided into three macrohabitat zones (east to west): (1) the shallow zone (3.8–8.5 m) was a steeply sloping boulder reef characterised by urchin barrens habitat with sparse *E. radiata*; (2) the kelp zone (8.5–10.6 m) was similar, however the lower third of the reef (adjoining the interface) was covered in a dense bed of *E. radiata*; (3) the barrens zone (10.6–12.2 m) sloped gently and was dominated by urchin barrens habitat.

Dent Rock (35°04' S, 150°41' E) is located on the south coast of NSW, with water temperatures ranging from 14° C (mean ± S.E.; 14.3° C ± 0.25; n=4) in July to 20° C (18.3° C ± 1.03; n=4) in November during this study. It is an elliptically shaped, shallow boulder reef surrounded by sand approximately 160 m offshore within the protected waters of Jervis Bay. Covering an area of 1935 m^2, the reef was divided into four macrohabitat zones: (1) quadrant 1 (5.3-6 m) sloped steeply and consisted of urchin barrens habitat replaced by *E. radiata* nearer the sand, with several low overhangs and sand-bottomed rock gutters; (2) quadrant 2 (5.2-5.3 m) sloped gently, with *E. radiata* near the sand and around several sand-bottomed gutters and barrens habitat in the upper reef; (3) quadrant 3 (5.2-5.5 m) was a gently sloping boulder reef with barrens habitat; (4) quadrant 4 (5.5-6 m) increased in slope from north to west and was mainly urchin barrens habitat with some *E. radiata* near the western edge.

Murray's Sandline (35°08' S, 150°46' E) is located within Jervis Bay. The site is a shallow seagrass bed located approximately 400 m offshore and within 2 km of the bay's mouth. The seagrass bed contained a mix of *Zostera capricorni* and *Halophila ovalis* with small patches of *Posidonia australis*. The eastern region of the bed extended for approximately 750 m and had a continuous cover of seagrass in a depth range of 11.4-4.2 m (west to east). At the western end the bed sloped steeply. The western region was approximately 750 m in length in depths of 11.4-6 m (east to west). Seagrass cover decreased and algae cover increased to the west. The sloping seagrass bed in both regions was divided into three macrohabitat zones. At the base of the bed was a gently sloping, barren sand area (hereafter called the sand zone) separated from the seagrass bed (the seagrass zone) by the interface zone. The interface zone was a 1 m wide transition between seagrass and sand zones comprised of a fragmented cover of seagrass.

Surveys

Surveys involved underwater visual census (UVC) surveys conducted at each location. To ensure maximum visual coverage, two experienced divers swam parallel to the reef/sand or seagrass/sand interface and approximately 1-2 m above the substrate. Only sharks observed resting when first sighted were utilised in this study to avoid possible bias from sharks in transit between locations.

Surveys commenced at Terrigal Haven in January 2002, at Cabbage Tree Harbour in July 2002 and at Dent Rock and Murray's Sandline in December 2002. Surveys concluded at all sites in December 2005. Terrigal Haven was surveyed twice weekly (one day and one night) during the adult onshore reproductive period (July to November; n=131 surveys) (hereafter

Table 1: Microhabitat variables and measurement methods for adult and juvenile resting site locations. Variables and measurement methods are identical unless specified as being for adult* or juvenile# resting sites.

Habitat Variable	Method
Distance (from interface)	Visual estimate (nearest 1 m*; 1 cm#)
Depth (m)	Dive computer (nearest 10 cm)
Temperature (° C)	Dive computer (nearest 0.1°C)
Reef slope	Depth/distance measures
Rock Cover (%)*	4m^2 visual quadrat
Algae/kelp cover (%)	4m^2 visual quadrat*; 0.25m^2 photoquadrat#
Sand cover (%)	4m^2 visual quadrat*; 0.25m^2 photoquadrat#
Seagrass cover (%)#	0.25m^2 photoquadrat
Total vegetation cover (%)#	0.25m^2 photoquadrat
Sediment grain size composition#	Sediment analysis

called the 'season') and at least monthly outside the season (n=45). Cabbage Tree Harbour was surveyed four times per month (2 day and 2 night) during the season (n=57) and monthly at other times (n=15). Dent Rock (n=33) and the eastern region of Murray's Sandline (n=29) were surveyed monthly during daylight hours. In addition, every three months from September 2003 to December 2005, surveys (n=10) were conducted over the 1.5 km length of the seagrass bed at Murray's Sandline.

Habitat Variables

Habitat usage was assessed at two levels. Macrohabitat was the general landscape-scale features (macrohabitat zones referred to above) inhabited by *H. portjacksoni*, whilst microhabitat variables (Table 1) were the finer-scale elements operating at the scale of individual sharks (Hall et al. 1997).

The macrohabitat zone occupied by all resting sharks at the time of first sighting was recorded at all sites. The total number of resting sharks for which habitat data was recorded in each year at Terrigal Haven (2002-2005) was 32, 24, 17 and 9; Cabbage Tree Harbour (2003-2005) was 26, 21 and 9; Dent Rock (2003-2005) was 33, 27 and 26; and, Murray's Sandline (2003-2005) was 169, 105 and 56.

The microhabitat variables (Table 1) of the positions used by resting adult sharks were quantified in a 2 x 2 m area (delimited by a quadrat) centred on the resting sharks and in haphazardly selected, unutilized positions of the same area. Microhabitat features were quantified at Terrigal Haven (35 resting sharks, 106 unutilised positions), Cabbage Tree Harbour (38 resting sharks, 75 unutilised positions), and Dent Rock (27 resting sharks, 121 unutilised positions). Microhabitat features of the resting positions of juvenile sharks (Table 1) in the seagrass nursery were determined at haphazardly selected (n=90) and utilised resting (n=20) positions spread over both regions of the seagrass bed using a 0.25 m^2 digital photographic quadrat (digital camera mounted on a preset quadrat frame). The image was analysed for percent cover (Table 1) using a one hundred point grid method, in which a 10 x 10 square grid was superimposed over the photograph and the percentage contribution of each feature within each square was visually estimated and individually summed (Foster et al. 1991). Sediment samples were also taken by drawing a 50 mm long by 30 mm diameter plastic container across the sediment to a maximum depth of 15 mm. The samples were subsequently dried at 60° C for 48 hr and sorted through a stacked series of graded sieves (1 mm, 500 µm, 212 µm, 63 µm, <63 µm) in a sediment shaker for 10 min. Sample fractions were weighed individually.

Egg capsules were found throughout the sites at Terrigal Haven and Dent Rock, however habitat data at the oviposition sites was only collected in 2004 and 2005. Primary oviposition areas were defined as concentrated areas (up to 15 m^2) with greater than 10 egg capsules. The habitat and microhabitat features (depth; reef slope; rock size; crevice size; and, crevice depth) at the site of each individual egg capsule and haphazardly selected, unutilised positions in both oviposition areas and other portions of the sites were recorded at Terrigal Haven (14 eggs; 30 unutilised positions) and Dent Rock (17 eggs; 40 unutilised positions).

Data Analysis

The macrohabitat zone occupied by individual resting *H. portusjacksoni* was recorded during each survey. Survey data was pooled by factor (e.g. zone, year, sex, diel period) and Likelihood Ratio (LR) tests were used to test the null hypothesis for each site that there was no significant difference in the proportion of resting sharks that utilised each macrohabitat zone. Separate LR tests were conducted for each year, sex and diel period for adults and for each year for juveniles. *G*-tests were used for pair-wise comparisons of significant LR results (Sokal and Rohlf 2003). The heterogeneity of egg capsule distribution was tested with *G*-tests by comparing the number of viable capsules located in the primary oviposition areas and other locations within each site. The viability of capsules was determined on the absence of predation or other physical damage (Rodda 2000; Powter 2006) or the visible presence of an embryo inside the capsule.

Microhabitat characteristics of individual adult and juvenile resting positions and the site of oviposited egg capsules were examined using Principal Components Analysis (PCA) in PRIMER 5 (PRIMER-E Ltd, UK). Prior to analyses, draftsman plots were utilised to ensure that variables were not highly inter-correlated (i.e. $R > 0.95$) (Clarke and Warwick 2001). Proportions were arcsine transformed and distances were $\log_e$ transformed before analysis (Sokal and Rohlf 2003).

The relative availability of each macrohabitat type was quantified from scaled underwater maps of each site's terrain (Powter 2006). Habitat preferences were determined from resource selection ratios (Manly et al. 1993) using the formula $\hat{w}_i = o_i / p_i$, where $\hat{w}_i$ is the preference score for habitat category i, o_i is the proportion of habitats used in category i and p_i is the proportional availability of habitat category i. Preference scores were standardised (B_i) to sum to

1, by dividing each preference score (w_i) by the sum of the preference scores for all habitat categories. The critical value of B (B_{CRIT}) related to the number of habitats as follows: B_i < (1/number of habitats) indicated avoidance and B_i > (1/number of habitats) indicated preference.

The null hypothesis that *H. portusjacksoni* selected habitats at random at each study site was tested using the χ^2 test with (n-1) degrees of freedom (Manly et al. 1993):

$$\chi^2 = 2\sum_{i=1}^{n}\left[u_i \ln\left(\frac{u_i}{Up_i}\right)\right]$$

and pair-wise tests of habitat selection ratios were conducted to determine any significant differences ($H_0 : \hat{w}_i = \hat{w}_j$) using the χ^2 test with 1 degree of freedom:

$$\chi^2 = \frac{(\hat{w}_i - \hat{w}_j)^2}{\mathrm{var}(\hat{w}_i - \hat{w}_j)}$$, and

$$\mathrm{var}(\hat{w}_i - \hat{w}_j) = \frac{o_i(1-o_i)}{Up_i^2} - \frac{2o_io_j}{Up_ip_j} + \frac{o_j(1-o_j)}{Up_j^2}$$

where, u_i is the number of sharks in habitat *i*; *U* is the total number of observations of sharks; o_i, o_j is the proportion of habitats used in category *i* or *j*; and, p_i, p_j is the proportional availability of habitat category *i* or *j*.

RESULTS

Adult Macrohabitat Utilisation

The macrohabitat zone utilised by resting sharks differed significantly at Terrigal Haven from 2003 to 2005 (Table 2). In 2002, the greatest proportion of sharks was located in the shallow zone, however this proportion declined from 2003 to 2005, with a shift to the barrens zone (Fig. 2a). There was no evidence of differential use of macrohabitat zones by males and females at Terrigal Haven (Table 2).

At Cabbage Tree Harbour there was no significant difference in the use of macrohabitat zones across survey years or by sex (Table 2, Fig. 2b). There were significant differences in the use of macrohabitat zones at Dent Rock across the survey years, but not across sexes (Table 2, Fig. 2c). In 2003, there was a greater proportion of resting sharks in quadrant 2 and the lowest relative proportion of sharks in quadrant 3 (Fig. 2c). The proportion of sharks in quadrant 1 in 2003 was also less than in 2005.

Diel utilisation of macrohabitat zones at Terrigal Haven differed only in 2004 (Table 3, Fig. 3a). In 2004 there were significantly more resting sharks in the shallow zone at night than during the day (*G*-test, d.f.=1, *P*=0.02). Diel utilisation of macrohabitat zones at Cabbage Tree Harbour differed only in 2005 (Table 3, Fig. 3b). However, only one resting *H. portusjacksoni* was recorded at night at Cabbage Tree Harbour in that year. Nocturnal surveys were not conducted at Dent Rock.

Adult Microhabitat Utilisation

The PC1 axis of the Principal Components Analysis (PCA) biplot for Terrigal Haven represents a gradient of decreasing cover of sand (left to right) and indicates selection of resting positions with moderate sand cover (55.6 ± 3.29%; mean ± SE) (Table 4, Fig. 4a). The PC2 axis represents a gradient of increasing reef slope (bottom to top) and indicates selection of resting positions of low to moderate reef slope. The tight clustering of resting positions compared to the unutilised positions, suggests sharks were very selective in their choice of resting position.

The PC1 axis of the PCA biplot for Cabbage Tree Harbour represents a gradient of decreasing cover of rock (left to right) and indicates selection of resting positions with moderate to high rock cover (87.0 ± 4.50%) (Table 4, Fig. 4b). The PC2 axis represents a gradient of decreasing kelp cover (bottom to

Table 2: Likelihood Ratio test (LR) results of macrohabitat zone utilisation for resting adult *H. portusjacksoni* at Terrigal Haven, Cabbage Tree Harbour and Dent Rock by year and sex.

	Terrigal Haven		Cabbage Tree Harbour		Dent Rock	
Comparison	LR	*P*	LR	*P*	LR	*P*
Zone x Year	21.14	0.002	4.21	0.379	14.94	0.021
Zone x Sex	3.88	0.143	0.39	0.820	6.17	0.104

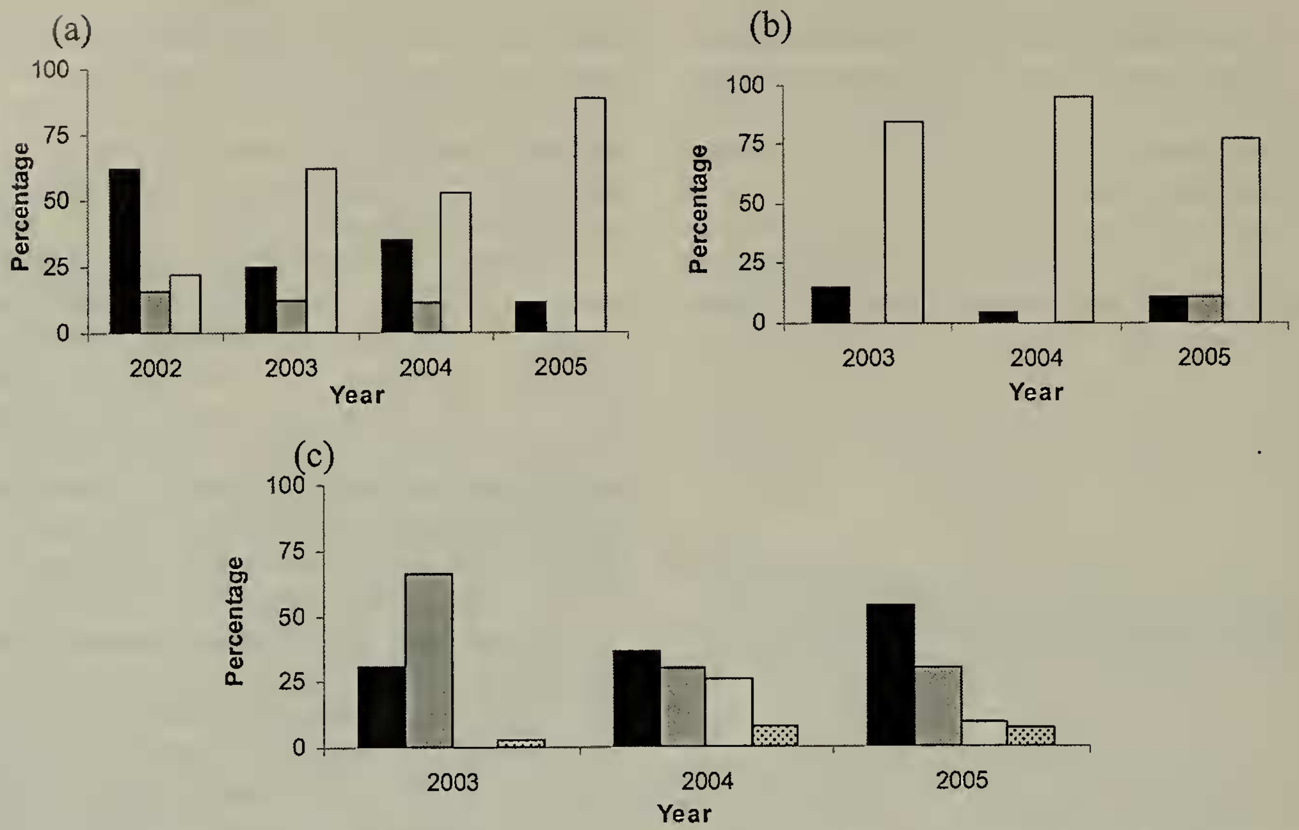

Figure 2: Percentage of resting adult *H. portusjacksoni* by year and macrohabitat zone at (a) Terrigal Haven (black bars = shallow; grey bars = kelp; white bars = barrens), (b) Cabbage Tree Harbour (black bars = wall; grey bars = boulder; white bars = gutter) and (c) Dent Rock (black bars = quadrant one; grey bars = quadrant two; white bars = quadrant three; stippled bars = quadrant four).

top) and indicates selected resting positions had low to moderate kelp cover (5.6 ± 2.04%). The PCA biplot for Dent Rock (Fig. 4c) displays a similar pattern to Cabbage Tree Harbour, with resting positions having moderate to high rock cover (48.0 ± 5.09%) and low to moderate kelp cover (16.5 ± 3.02%).

Adult Habitat Preferences

Although the interface accounted for only 5% of the available habitat at Terrigal Haven, resting adult *H. portusjacksoni* exhibited a highly significant preference for this habitat (Table 5). This pattern was consistent across all years and both sexes. The sand and kelp habitats were avoided in all years (all B_i<0.25).

Table 3: Likelihood Ratio test (LR) results for the number of resting adult *H. portusjacksoni* by diel period and macrohabitat zone at Terrigal Haven (TH) and Cabbage Tree Harbour (CTH) by year. ^{ns}P>0.05; * P<0.05; ** P<0.01

		2002		2003		2004		2005	
Site	Zone	% Day	LR	% Day	LR	% Day	LR	% Day	LR
TH	Shallow	35.0		33.3		0		0	
	Kelp	20.0	2.84^{ns}	66.7	0.92^{ns}	100	12.05^{**}	0	0.87^{ns}
	Barrens	66.7		46.7		66.7		37.5	
CTH	Wall			50.0		100.0		100.0	
	Boulder			0.0	1.33^{ns}	0.0	0.69^{ns}	0.0	6.28^{*}
	Gutter			86.4		70.0		100.0	

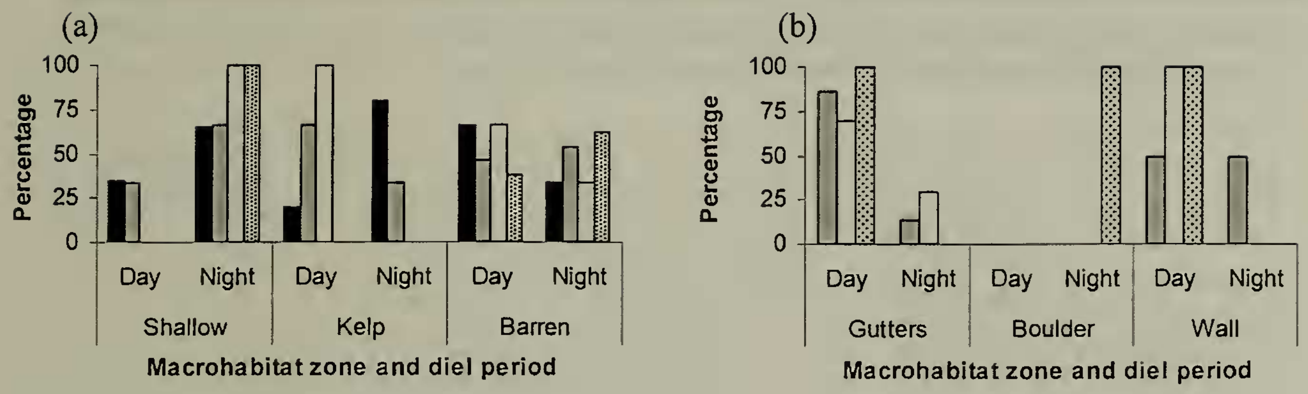

Figure 3: Diel distribution of resting adult *H. portusjacksoni* by year and zone at (a) Terrigal Haven and (b) Cabbage Tree Harbour for 2002 (black bars), 2003 (grey bars), 2004 (white bars) and 2005 (stippled bars).

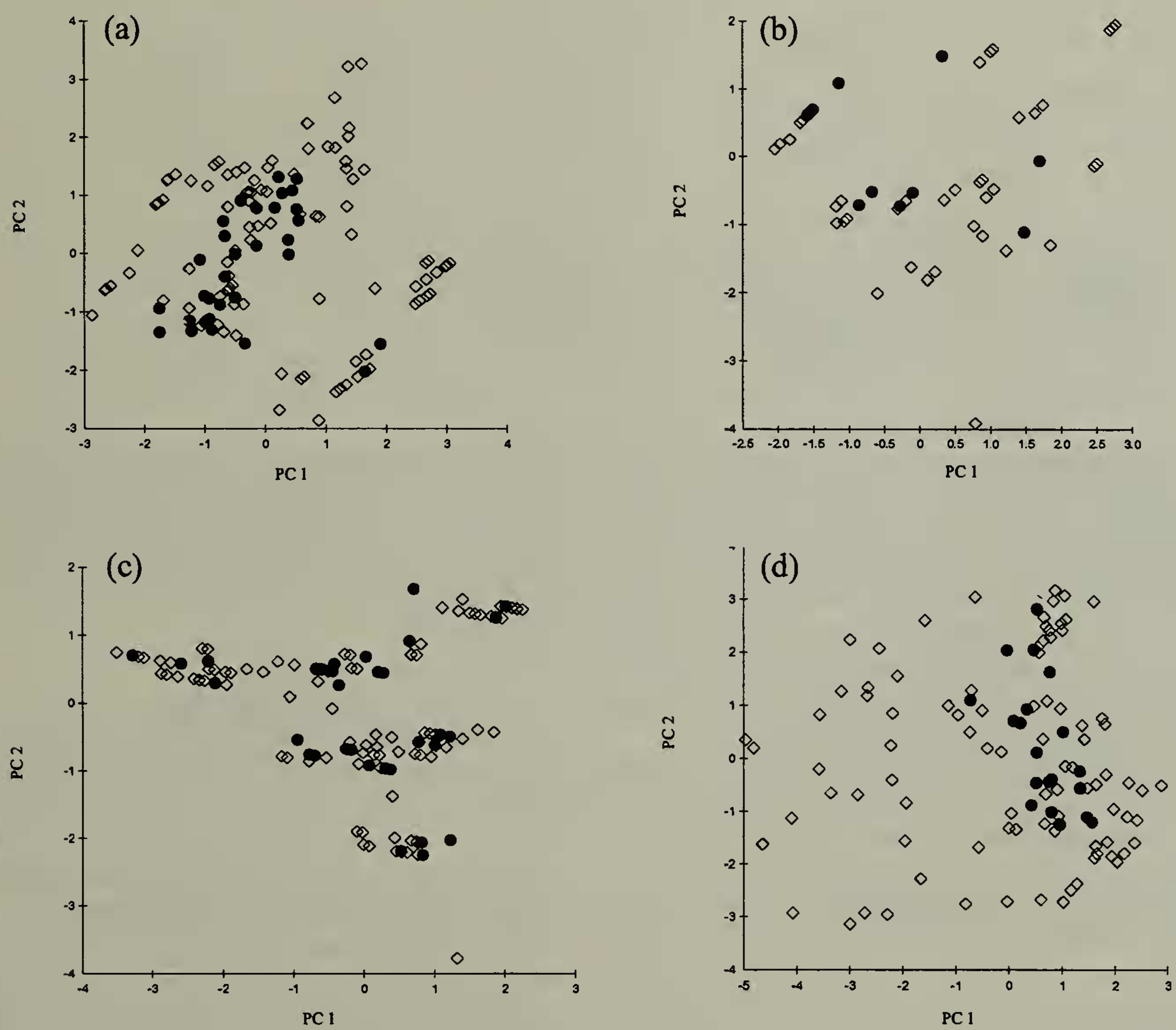

Figure 4: PCA biplots of microhabitat variables utilised by resting *H. portusjacksoni* (closed circles) and random unutilised locations (open diamonds) for adults at (a) Terrigal Haven (PC1, sand cover; PC2, reef slope), (b) Cabbage Tree Harbour (PC1, rock cover; PC2, kelp cover) and (c) Dent Rock (PC1, rock cover; PC2, kelp cover) and juveniles at (d) Murray's Sandline (PC1, 500 µm sediment fraction; PC2, seagrass cover).

Table 4: PCA results for microhabitat variables utilised by resting adult *H. portusjacksoni* at Terrigal Haven, Cabbage Tree Harbour and Dent Rock and juveniles at Murray's Sandline. The variables with the highest eigenvalues for each axis are shown.

Site	PC	Variable	Eigenvector	Variation (%)	Cumulative Variation (%)
Terrigal Haven	1	Sand Cover	-0.603	39.8	39.8
	2	Reef Slope	0.630	32.2	72.0
	3	Kelp Cover	-0.776	20.5	92.5
Cabbage Tree Harbour	1	Rock Cover	-0.613	45.0	45.0
	2	Kelp Cover	-0.713	28.8	73.8
	3	Reef Slope	-0.762	16.3	90.1
Dent Rock	1	Rock Cover	-0.623	46.6	46.6
	2	Kelp Cover	-0.860	24.6	71.2
	3	Reef Slope	0.984	20.3	91.4
Murray's Sandline	1	500 μm Sediment	-0.468	33.6	33.6
	2	Seagrass Cover	0.211	27.6	61.2
	3	Reef Slope	0.623	13.7	74.9

At Cabbage Tree Harbour the gutter habitat was significantly preferred by resting adult female *H. portusjacksoni* in all years (Table 5). Resting males generally exhibited a preference for the interface habitat with the exception of 2003. However, the number of resting males at Cabbage Tree Harbour was very low, with only seven observed during the three study years. No resting individuals of either sex were ever observed in the sand or kelp habitats.

At Dent Rock adult female *H. portusjacksoni* generally preferred resting in the gutter habitat, whilst males mainly preferred the interface habitat (Table 5). However, there were some variations to this pattern. Although there was a moderate preference for the gutter habitat (B_i=0.32) by resting males in 2005, there was a significantly greater preference for the interface habitat (B_i=0.68; χ^2-test, d.f.=3, P<0.001). In 2004 and 2005, the preferred resting habitat for adult female *H. portusjacksoni* was the gutter habitat. In both years this habitat was significantly preferred over the remaining four habitat types. However, in 2003 female habitat preferences were approximately equally shared between the interface (B_i=0.51) and the gutter (B_i=0.49) habitats and were not significantly different (χ^2-test, d.f.=3, P=0.60). A small preference for the interface habitat was also exhibited by females in 2005 (B_i=0.23), but the preference for the gutter habitat was significantly greater (B_i=0.77; χ^2-test, d.f.=3, P<0.001).

Juvenile Macrohabitat Utilisation

Overall there was no significant difference in the proportion of resting juvenile *H. portusjacksoni* located in the east or west macrohabitat zones (ANOVA, d.f.=1,52, *P*=0.23), however, this was due to a reversal in proportions observed in 2005 when 65.2% of resting juveniles occurred in the western zone. In the years 2003 and 2004 there were significantly more juveniles observed resting in the east (85.6% and 85.4%, respectively) than the west macrohabitat zone (*t*-test, d.f.=1, *P*<<0.01). During these years, there was approximately 6 times the number of resting juveniles in the east macrohabitat zone than the west.

Table 5: Macrohabitat type and proportional availability (p_i) with preferred habitat type ([a]) and standardised preference scores (B_i) by year and sex at Terrigal Haven, Cabbage Tree Bay, Dent Rock and Murray's Sandline. B_i > [#] (site B_{CRIT} value) indicates a significant preference.

Availability		Preferences								
Habitat	p_i		2002		2003		2004		2005	
Terrigal Haven ([#] 0.25)										
		Sex	Habitat[a]	B_i	Habitat[a]	B_i	Habitat[a]	B_i	Habitat[a]	B_i
Barren	0.34	Male	Interface	0.95	Interface	0.94	Interface	0.87	Interface	1.00
Interface	0.05	Female	Interface	0.96	Interface	0.92	Interface	0.89	Interface	0.84
Kelp	0.19	Combined	Interface	0.96	Interface	0.93	Interface	0.89	Interface	0.93
Sand	0.42									
Cabbage Tree Harbour ([#] 0.2)										
Barren	0.41	Male			Gutter	0.64	Interface	1.00	Interface	1.00
Gutter	0.01				Interface	0.34				
Interface	0.05	Female			Gutter	0.98	Gutter	0.99	Gutter	0.93
Kelp	0.08	Combined			Gutter	0.95	Gutter	0.98	Gutter	0.87
Sand	0.45									
Dent Rock ([#] 0.2)										
Barren	0.38	Male			Interface	0.86	Gutter	0.57	Interface	0.68
Gutter	0.06						Interface	0.35	Gutter	0.32
Interface	0.05	Female			Interface	0.51	Gutter	0.78	Gutter	0.77
Kelp	0.12				Gutter	0.49			Interface	0.23
Sand	0.39	Combined			Interface	0.58	Gutter	0.57	Gutter	0.57
					Gutter	0.42	Interface	0.32	Interface	0.43
Murray's Sandline ([#] 0.33)										
Interface	0.10	Male			Interface	0.95	Interface	0.91	Interface	0.93
Sand	0.45	Female			Interface	0.95	Interface	0.95	Interface	0.94
Seagrass	0.45	Combined			Interface	0.95	Interface	0.94	Interface	0.94

Juvenile Microhabitat Utilisation

The PC1 axis of the PCA biplot represents a gradient of decreasing percentage of the 500 μm sediment fraction (left to right) and indicates that juveniles utilised resting positions with a low percentage of this sediment fraction (3.2 ± 0.22%; mean ± SE) (Table 4, Fig. 4d). The PC2 axis represents a gradient of increasing seagrass cover (bottom to top) and indicates selection of resting positions with moderate seagrass cover (38.0 ± 4.92%). The shark resting locations are relatively tightly clustered in respect of the two PC axes in comparison to the broadly spread unutilised locations, suggesting juveniles were very selective in the choice of resting locations.

Juvenile Habitat Preferences

Resting juveniles exhibited a very strong preference for the interface habitat (Table 5). This preference was demonstrated by both sexes and in all years. Although the B_i values for the seagrass habitat were small (female: 0.05 ± 0.003; male: 0.07 ± 0.013; mean ± SE), the preference scores were significantly

Table 6: Principal Components Analysis results for key oviposition microhabitat variables at Terrigal Haven and Dent Rock. Variables with the highest eigenvalue shown for each axis.

Site	PC	Variable	Eigen-vector	Variation (%)	Cumulative Percentage
Terrigal Haven	1	Reef Slope	-0.557	47.4	47.4
	2	Rock Size	0.795	23.2	70.6
	3	Crevice Depth	0.624	14.2	84.7
Dent Rock	1	Crevice Depth	-0.589	33.9	33.9
	2	Crevice Width	0.713	25.5	59.4
	3	Rock Size	0.850	17.1	76.5

higher than the sand habitat for both sexes in all years.

Oviposition Site Habitat Characteristics

Viable egg capsules were not uniformly distributed across the reef. Significantly more viable egg capsules occurred in the single primary oviposition area at both Terrigal Haven and Dent Rock in 2004 (*G*-tests, df=1, P=0.02; df=1, P=0.02, respectively) and 2005 (*G*-tests, df=1, P<0.001; df=1, P=0.03, respectively) than elsewhere on these reefs. The same primary oviposition area at each site was used in both years.

The PC1 axis of the PCA biplot for Terrigal Haven represents a gradient of decreasing reef slope (left to right) and indicates that *H. portusjacksoni* placed their eggs in a steeply sloping portion of the reef (25-30°) (Table 6, Fig. 5). The PC2 axis represents a gradient of increasing rock size (bottom to top), indicating that selected oviposition sites were in an area with small rocks (51.6 ± 5.23 cm; mean ± SE). At Dent Rock, the PC1 axis represents a gradient of decreasing crevice depth (left to right) and indicates that oviposition sites with moderate crevice depth (42.2 ± 7.40 cm) were utilised. The PC2 axis represents a gradient of increasing crevice width (bottom to top) showing that utilised oviposition sites had moderate to narrow crevices (13.2 ± 1.11 cm). The utilised oviposition locations are relatively tightly clustered in respect of the two PC axes at both Terrigal Haven and Dent Rock in comparison to the broadly spread unutilised locations, suggesting high selectivity in the choice of oviposition locations.

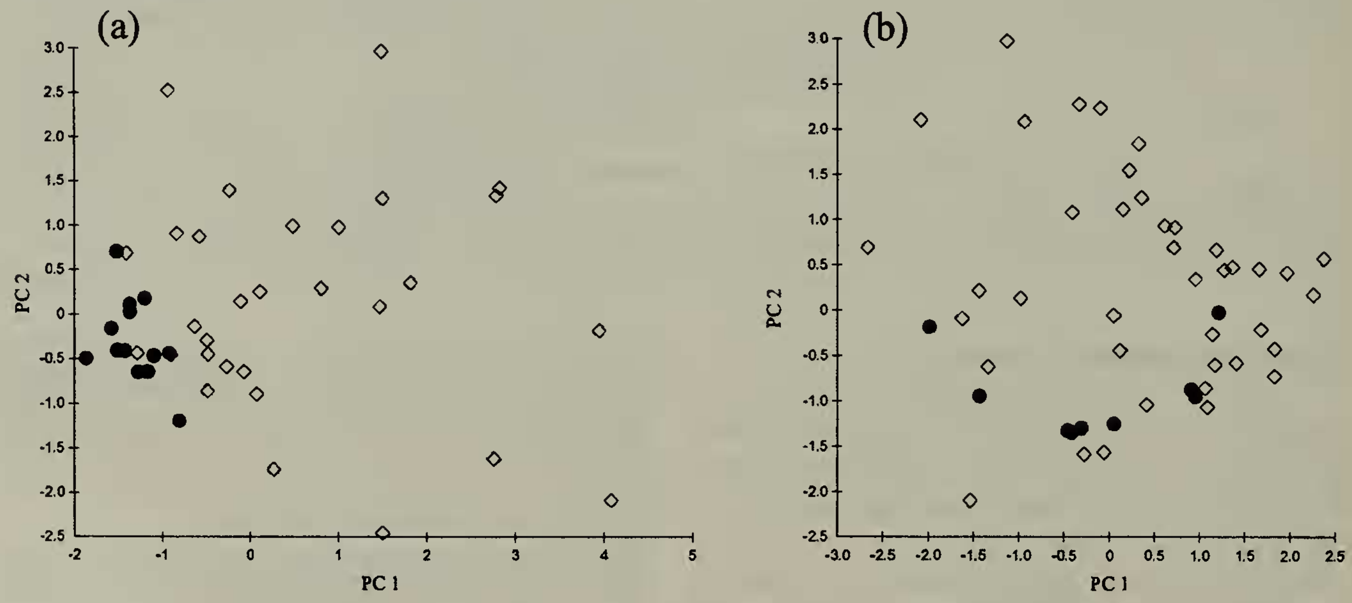

Figure 5: Principal Components Analysis plots of microhabitat variables at positions with egg capsules (closed circles) and random positions without egg capsules (open diamonds) at (a) Terrigal Haven (PC1, reef slope; PC2, rock size) and (b) Dent Rock (PC1, crevice depth; PC2, crevice width).

Table 7: Macrohabitat type, proportional availability (p_i) and standardised preference scores (B_i) for oviposition sites at Terrigal Haven and Dent Rock for all years combined. * indicates preferred habitat (Terrigal Haven $B_i > 0.33$; Dent Rock $B_i > 0.25$).

Terrigal Haven		
Habitat	p_i	B_i
Shallow*	0.357	0.522
Kelp	0.304	0.156
Barrens	0.339	0.322

Dent Rock		
Habitat	p_i	B_i
Quadrant 1	0.126	0.200
Quadrant 2	0.385	0.010
Quadrant 3	0.371	0
Quadrant 4*	0.118	0.791

At Terrigal Haven, the shallow macrohabitat zone was significantly preferred as an oviposition site (Table 7). The barrens zone was marginally below the B_{CRIT} level of habitat preference (0.33), but was still significantly selected over the kelp zone. Quadrant 4 macrohabitat zone at Dent Rock was the significantly preferred oviposition habitat (Table 7). Quadrant 1 was marginally below the B_{CRIT} level of preference (0.25), but was significantly selected over quadrants 2 and 3.

DISCUSSION

To obtain a sufficiently detailed understanding of habitat requirements for use in conservation and management, habitat studies must address two key issues: a determination of how sharks distribute themselves among the available habitats and an understanding of the reasons for these choices and selections (Sims 2003). This study addressed the issue of distribution across habitats at geographically separate locations and explored the second issue in relation to the resting habitat of *H. portusjacksoni*. Despite differences in UVC frequency at adult sites, surveys were conducted over several years, across the entire breeding season, at different times of day and across a range of weather conditions to ensure that observations were representative.

Adult Habitat Utilisation and Preferences

The interface habitat was strongly preferred at Terrigal Haven by resting *H. portusjacksoni*. McLaughlin (1969) found that 88% of all adult *H. portusjacksoni* in captive studies rested within 1.2 m of the pool sides and suggested that this may have been to maximise the sunlight shading effects of the edges. Nelson and Johnson (1970) and Strong (1989) reported that adult *Heterodontus francisci* were mainly found sheltering in caves and overhangs during the day to avoid exposure to strong sunlight. It is unlikely that this is a factor for adult *H. portusjacksoni* at Terrigal Haven as the east-west running interface is exposed to unobstructed sunlight throughout the day. Additionally, there was no diel variation in the use of, or preference for, this habitat. A more plausible explanation for the preference for the interface habitat is related to the avoidance of strong water movement. The Terrigal Haven site was located on the leeward side of the reef and is afforded significant protection from all but large seas (personal observations). Resting positions were concentrated into two small patches in the shallow zone, corresponding to the most steeply sloping portion of the reef, and barrens zone, which is the deepest area. It is likely that by resting close to the reef interface, *H. portusjacksoni* are minimising their exposure to water movement by using the reef as a form of flow refuge (Webb 1989). Similarly, resting adult sharks at Dent Rock were mainly encountered on the reef's more sheltered southern side in quadrants 1 and 2.

Heterodontus francisci are known to migrate to deeper water during the more storm-prone winter months around California and shark numbers were reduced during surveys following high seas (Strong 1989). Similarly, Farina and Ojeda (1993) suggest that redspotted catsharks, *Schroederichthyes chilensis*, migrate into deeper water during winter to avoid strong water movement and turbulence. Epaulette sharks, *Hemiscyllium ocellatum*, on shallow reef flats were often observed underneath or directly behind coral heads, which may be used as 'flow refuges' from currents (Peach 2002).

The presence of numerous rock and rock/sand gutters at Dent Rock represents a significant difference between Dent Rock and Terrigal Haven, as does the sex-based variation in habitat use at the former site. Males at Dent Rock were significantly more likely to prefer resting positions at the interface than in the gutters, whilst females exhibited a strong preference for the gutters. Sims et al. (2001) reported that female dogfish, *Scyliorhinus canicula*, were often found in female-only aggregations in refuge habitats to decrease their accessibility by males and reduce the energetically demanding activity of mating. This male avoidance strategy is likely to be a significant factor in the utilisation of gutters by females at Dent Rock. The gutters are narrow and provide limited access from the sides and are often occupied by groups of females in close contact with each other. Sims et al. (2001) found that male *S. canicula* frequented the entry/exit points of the female refuges at times when females were more likely to be coming or going. At Dent Rock, male *H. portusjacksoni* were more likely to occupy resting positions outside, but adjacent to, the gutters, presumably to be near females if mating opportunities arose. On a number of occasions a single male *H. portusjacksoni* was observed resting several metres from the interface where a group of females were resting in close proximity to each other. Although the females were in a mixed orientation to each other, the male was always perpendicular to, and facing, the females.

Habitat preferences of resting *H. portusjacksoni* at Cabbage Tree Harbour conform to both the water movement and male avoidance strategies. The reef face is completely exposed to the prevailing seas and is often significantly affected by strong swell and surge (personal observations). As expected by the water movement avoidance strategy, the number of adult *H. portusjacksoni* resting at the interface at Cabbage Tree Harbour was low. Females exhibited a highly significant preference for the rock gutters in the deeper, eastern end of the reef and avoided the remaining habitats. The strong preference exhibited by females for the gutters at Cabbage Tree Harbour also supports the male avoidance strategy, with over 90% of resting females located in the gutters. On the contrary, only one male *H. portusjacksoni* was observed resting in the gutters during the three survey years, whilst 50% (n=14) of all males sighted at Cabbage Tree Harbour were actively swimming in the gutter zone.

Juvenile Habitat Utilisation and Preferences

The habitat utilised by juvenile *H. portusjacksoni* is totally distinct from that of the adults. Despite three to four years surveying adult habitats at Terrigal Haven, Cabbage Tree Harbour and Dent Rock, juvenile sharks were never observed at these sites. Instead juvenile sharks were located in a shallow seagrass bed at Murray's Sandline geographically isolated from the rocky reefs typically utilised by the adults. Such spatial separation of adults and juveniles is common to many elasmobranchs (Merson and Pratt 2001; Pratt and Carrier 2001; Carlson 2002). Fulfilling the three criteria specified by Heupel et al. (2007), this site can be considered a nursery area for *H. portusjacksoni*. Juveniles were encountered here regularly, but not at other sites used by adults; they spend extended periods of time at the site; and, exhibit strong site fidelity for the site over several years (Powter 2006).

Juvenile *H. portusjacksoni* made significantly greater use of the eastern portion of the seagrass bed. The eastern portion accounted for 50% of the total surveyed area, however, 81.7% of sharks were located within the eastern portion of the seagrass bed. Although this pattern was consistent in 2003 and 2004, it was reversed in 2005. The exact reason for this shift is unclear, but may be related to an avoidance of strong water movement. During a survey of the entire seagrass bed in March 2004 a lower than expected number of juvenile *H. portusjacksoni* was located (Powter 2006). All of the juveniles located in the eastern portion of the bed during this survey were in the easternmost two-thirds of the bed and closer to Bowen Island than previous surveys. Whilst surveying the midwestern zone, a 100 m section of the seagrass bed was missing after being washed away in heavy seas several weeks previously. An identical observation was made in December 2005 where an extensive area further east of the previous section had been washed away. Again the number of juvenile *H. portusjacksoni* was significantly lower than expected.

Murray's Sandline is afforded some protection from the prevailing seas by the southern headland of Jervis Bay (Bherwerre Peninsula) and Bowen Island. However, the western portion of the bed is less protected due to its alignment with the gap between Bowen Island and Bherwerre Peninsula. Hence the reduction in juvenile numbers after these storm events indicates that juveniles, like the adults, may adopt a strategy of avoiding strong water movements. Further support for this notion is the significant role sediment grain size and bed slope plays in the selection of resting sites. Bed slope, greatest in the lee of Bowen Island, is likely to impact on the intensity of water movement, with the juveniles occupying resting positions at the base of the steepest sloping portion of the eastern seagrass bed, which they may use as flow refuges to assist in station holding (Webb 1989). The reduced proportion of the 500μm grain size fraction at juvenile resting sites was also likely to be related to gross water movement, as seagrass is known to influence both the velocity and direction of moving water. Low stem densities can lead to substrate erosion, whilst higher densities can facilitate the settling out of suspended particles (Edgar 2001).

Although many studies have defined nursery areas and their importance to elasmobranchs, few have addressed the issue of habitat preference

(Simpfendorfer and Heupel 2004). Both within and between years and seasons, there was no difference in the strong preference resting juveniles exhibited for the interface habitat, where they rested on the sand substratum in close proximity to the seagrass bed. This narrow strip connecting the sand flat to the seagrass bed comprised only 10% of the surveyed area, but accounted for 83.3% of all juvenile *H. portusjacksoni*. Strong (1989) observed a similar pattern in juvenile *H. francisci* which exhibited a strong preference for sand substratum and often sheltered near scattered algae, debris or other topographic features. Habitat edges and ecotones have been shown to be important to a diverse array of organisms for a wide range of reasons (Meffe and Carroll 1997). However, a possible benefit of the interface habitat to juvenile *H. portusjacksoni* relates to the visual complexity of this region and the juvenile's disruptive colouration. Motionless juveniles at the interface were often difficult to detect and blended well with their surroundings (personal observations). The preference may also arise from a resolution of the conflict between a habitat being too complex for effective foraging and one not providing sufficient refuge (Adams et al. 2004). The diet of juvenile *H. portusjacksoni* is dominated by benthic invertebrates, such as decapod crustaceans and echiurans (Powter 2006) and the seagrass bed is likely to provide a suitable source of these prey items (Edgar 2001). During UVC surveys juveniles were observed on at least four occasions foraging in the substrate of the seagrass bed or on the epiphytic organisms on the seagrass blades. However, juveniles avoided swimming amongst the closely spaced seagrass blades and were infrequently found resting amongst them. Accordingly, the interface habitat may provide an appropriate balance of adequate refuge with reasonable proximity to prey and ease of access to foraging, but at a decreased likelihood of impediments to free movement.

Oviposition Habitat Utilisation and Preferences

As an oviparous species, *H. portusjacksoni* deposits its egg capsules in rock crevices in the same shallow rocky reefs where adults are found resting (McLaughlin and O'Gower 1971). The choice of suitable habitat for oviposition is critical as the developing embryo spends 9-12 months within the capsule prior to eclosion (Rodda 2000). Oviposition occurred selectively within primary oviposition areas at Terrigal Haven and Dent Rock over at least two consecutive seasons, but there was no evidence of this activity at Cabbage Tree Harbour. Significant differences existed between Dent Rock and Cabbage Tree Harbour in terms of crevice width and depth, but no such differences existed between Terrigal Haven and Cabbage Tree Harbour (Powter 2006). However, the oviposition areas at Terrigal Haven (southern reef face) and Dent Rock (west-north-west reef face) were both located on the reef face less exposed to prevailing seas and on a downward sloping reef face behind a raised reef crest, whilst the reef at Cabbage Tree Harbour faced north and was significantly more exposed. Despite these similarities, the selected oviposition sites at the two locations did vary. The mean crevice width and depth at Dent Rock were significantly greater than at Terrigal Haven (Powter 2006) and the method of securing capsules was influenced by this. At Terrigal Haven capsules were predominantly located singly tightly wedged into crevices between rocks, with a maximum of two capsules observed in the same crevice. Hence, the narrower and shallower crevices at Terrigal Haven were suitable for securing individual egg capsules. Offering less opportunity to secure capsules in this way, the deeper, wider crevices at Dent Rock often contained multiple capsules laying relatively loose in the bottom of deep, narrow crevices, with a maximum of 18 capsules in the same crevice. Both of these methods served to hinder mechanical dislocation, but also offered protection from larger predators (Powter 2006). Additionally, both crevice types appeared to be equally effective at protecting egg capsules as demonstrated by the similar levels of embryonic mortality occurring at Terrigal Haven and Dent Rock (Powter 2006).

Hence, areas sheltered from the prevailing seas and with suitable crevices to prevent mechanical dislocation and predation appear to be a primary requirement for oviposition areas. However, suitable oviposition habitat could also be influenced by water temperature, which Rodda (2000) found had a significant effect on the early stages of embryonic development of *H. portusjacksoni* in laboratory experiments. The lower thermal limit fell between 15° and 18° C, whilst the upper thermal limit was approximately 22° C. Consequently the location of oviposition areas in shallow water may assist in optimal temperature regulation. Additionally, water temperature was found to be negatively correlated with adult *H. portusjacksoni* numbers at Terrigal Haven and Dent Rock, but not at Cabbage Tree Harbour (Powter 2006). McLaughlin and O'Gower (1971) also reported an inverse relationship between water temperature and *H. portusjacksoni* numbers, but did not offer an explanation for this relationship. The most likely reason is the narrow temperature tolerance of developing *H. portusjacksoni* embryos. Congregating on shallow coastal reefs for reproductive purposes (Powter 2006) it is likely that adult numbers at oviposition reefs, such as Terrigal Haven and Dent Rock, are related to temperatures within the optimal range for their developing offspring. The lack of both reproductive activity at Cabbage Tree Harbour and a relationship between shark numbers and water temperature is also consistent with this finding.

A significant preference for the two primary oviposition areas at Terrigal Haven and Dent Rock occurred over two consecutive seasons. Although repeated, or 'traditional', use over a number of breeding seasons by individual females could not be demonstrated, the high site fidelity exhibited by mature females at the reefs (Powter 2006) and the 'traditional reuse' of the oviposition sites suggests that females have strong philopatric links to the oviposition areas. Female *H. portusjacksoni* have a long reproductive life and 'experienced' females could reuse the same primary oviposition areas in subsequent years or dominant females may utilise the primary oviposition areas and subordinate females use other locations within the reef. Nonetheless this is the first quantitative determination of the use of traditional oviposition sites by an oviparous elasmobranch.

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